Buller

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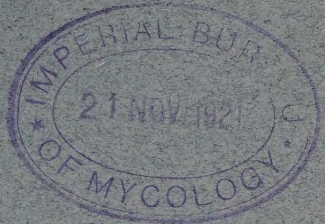

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THE PRODUCTION AND LIBERATION OF SPORES IN THE GENUS COPRINUS.

By Professor A. H. Reginald Buller, D.Sc., Ph.D., F.R.S.C.

A lecture with the above title was delivered before the British Mycological Society at its annual meeting in September last. The following are some of the observations which were mentioned.

In the Agaricineae there are two distinct spore-producing and spore-liberating types of fruit-body—the Coprinus type and the Mushroom type—which differ from one another in several structural, functional, and developmental details. The Coprinus type is specialized whilst the Mushroom type is generalized. There is evidence to show that, in the course of evolution, the latter has given rise to the former. Among the more highly evolved species of Coprinus may be mentioned:—*Coprinus atramentarius*, *C. narcoticus*, *C. stercorarius*, and *C. macrorhizus*, all of which possess cystidia, and *C. comatus* and *C. sterquilinus* which do not. In the first group of species the cystidia serve to keep the delicate gills apart, so that the spores on hymenial surfaces of adjacent gills are prevented from touching one another during development. On the other hand, in the second group of species, where cystidia are absent, the separation of the gills is provided for by the free margins of the gills which are swollen into sterile bands or flanges.

In *Coprinus atramentarius* the gills are *parallel-sided*, and thus differ from those of the Mushroom, etc., which have their sides inclined like the sides of the blade of a pen-knife. The parallel-sidedness of the gills in this and other species of Coprinus permits of the gills having considerable depth, and yet of being constructed with much less material than equally deep gills of the Mushroom and other Fungi of the Mushroom type.

In the Mushroom, etc., owing to the gills being shaped like the blade of a pen-knife and being positively geotropic, under normal conditions every part of the investing hymenium looks more or less downwards towards the earth. This enables every part of the hymenium (every square mm.) to produce and liberate spores successfully at the same time. In *Coprinus atramentarius*, on the other hand, on account of the gills being parallel-sided and incapable of giving a positively geotropic response to the stimulus of gravity, it is not possible for both sides of a gill to look downwards at the same time. Usually one side looks slightly downwards and the other slightly upwards. It would not, therefore, be possible for such a gill to liberate spores from

every part of its hymenium successfully at the same time. The spores on the surface inclined slightly upwards, after being shot out into the interlamellar space, would fall on to the gill, adhere there, and be lost.

The successful liberation of the spores from the parallel-sided gills of *Coprinus atramentarius* is brought about by special adaptations of which the following are the chief:—(1) The spores ripen in a progressive zone from below upwards on each gill. (2) The spores are discharged in succession from below upwards on each gill. (3) The spore-freed portions of the gills, as soon as they have come into existence, are destroyed by autodigestion. It takes from one to two days in *C. atramentarius* for the zone of spore-discharge, with the closely-following spore-freed zone and autodigestion zone, to move upwards from the bottom to the top of each gill. The spore-freed portions of the gills which are of no service to the fruit-body, are removed by autodigestion out of the way of the falling spores, and are thus prevented from becoming mechanical hindrances to the escape of the spores still being discharged. The zone of spore-discharge is always less than 0·5 mm. above the free gill edge. Since the spores are shot outwards into the interlamellar spaces to a distance of about 0·1 mm., and since they only have to fall downwards a distance of about 0·33 mm. between the gills before reaching the exterior of the fruit-body, they are able to escape from both sides of a gill even when this happens to be tilted to an angle of several degrees. Autodigestion (deliquescence) of the gills, which for so long was merely a meaningless and puzzling phenomenon, is now seen to be a necessary and important factor in bringing about successful spore-liberation in the Coprinus type of fruit-body.

The hymenium in the genus Coprinus (neglecting the cystidia which are present in some species and absent in others) consists of fertile basidia and of definite, constantly-occurring, sterile paraphyses. The latter function as *spacial agents* in that they prevent the spores of adjacent, simultaneously-maturing basidia from touching one another.

The writer discovered in the spring of 1911* that the basidia of most species of Coprinus *(C. atramentarius, C. comatus, C. sterquilinus, C. stercorarius,* etc.*)* are *dimorphic.* Long obviously-protuberant basidia and short practically non-protuberant basidia are interspersed among one another and the paraphyses so as to form a mosaic-work which is of such a kind that the spores of the long basidia are further from the surface of the hymenium than the spores of the short basidia, and so that they frequently overlap the latter without touching them. The

* In my "Researches on Fungi," Longmans, Green & Co., London, 1909, only the long, protuberant basidia are shown in the drawings of the hymenium of *Coprinus comatus.* The short basidia were left out, as they were then thought to be exceptional. Illustrations of the hymenium of various species of Coprini with correct details concerning the dimorphism of the basidia are in course of preparation for publication.

dimorphism of the basidia permits of a closer packing of the basidia on the hymenium than would otherwise be possible. Hymenial space is thus economised for spore-production. It was observed in *Coprinus sterquilinus* and *C. comatus* that in the zone of spore-discharge which proceeds upwards on each gill, the long basidia discharge their spores a short time before the immediately-adjacent short basidia. The spores of the short basidia, at the time when they are shot out into the interlamellar spaces, are thus prevented from colliding with the spores of the long basidia. In *C. micaceus* the basidia are more or less *trimorphic.*

The dimorphism and trimorphism of basidia are reminiscent of the dimorphism and trimorphism of stamens which in numerous flowers are beautifully significant in the process of cross-pollination.

Until discovering the fact of the dimorphism of the basidia, I was puzzled as to the significance of the striking protuberancy of Coprinus basidia. Now that the advantage gained by this protuberancy has been explained, the conclusion seems inevitable that such a fruit-body as that of *Coprinus atramentarius* is organized even in regard to the minutest details of the structure and function of its parts, so that it may attain the highest efficiency as a whole in the production and liberation of its spores.

I have noticed that the mycelium of Coprini (also that of many other Fungi) retains its vitality when dried in the medium in which it is growing. At the September Meeting of the British Mycological Society, I requested that members would be so good as to send me species of Coprinus in the mycelial condition. Since the meeting Miss E. M. Wakefield has sent me two species which she found growing on sticks at Kew. The sticks were simply allowed to dry and were forwarded to me at Winnipeg. On their arrival they were moistened, and new fruit-bodies soon came up. I was therefore enabled to make a careful study of these species and to determine their macroscopic and microscopic characters. Both species proved of interest. One, which may perhaps be called *Coprinus bisporigera,* has but two spores on each basidium as a rule, but a small proportion of the basidia have just one spore each. The unisporigerate basidia possess spores about twice as large as those produced by the bisporigerate basidia. The other species which perhaps may be called *Coprinus echinosporus* has distinctly echinulate spores. Mr. A. D. Cotton has sent me a species in dried dung which is also yielding fruit-bodies. Mr. T. Petch has provided me with a species which may be *Coprinus domesticus.* To the senders of the material just mentioned I am much indebted and here wish to express to them my best thanks. I should be glad to receive further material, as in the course of time I hope to give a comparative account of the Coprini.